

A Modern Human Humerus From the Early Aurignacian of Vogelherdhöhle (Stetten, Germany)

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ABSTRACT Implicit in much of the discussion of the cultural and population biological dynamics of modern human origins in Europe is the assumption that the Aurignacian, from its very start, was made by fully modern humans. The veracity of this assumption has been challenged in recent years by the association of Neandertal skeletal remains with a possibly Aurignacian assemblage at Vindija Cave (Croatia) and the association of Neandertals with distinctly Upper Paleolithic (but non-Aurignacian) assemblages at Arcy-sur-Cure and St. Césaire (France). Ideally we need human fossil material that can be confidently assigned to the *early* Aurignacian to resolve this issue, yet in reality there is a paucity of well-provenanced human fossils from early Upper Paleolithic contexts. One specimen, a right humerus from the site of Vogelherd (Germany), has been argued, based on its size, robusticity, and muscularity, to possibly represent a Neandertal in an Aurignacian context. The morphological affinities of the Vogelherd humerus were explored by univariate and multivariate comparisons of humeral epiphyseal and diaphyseal shape and strength measures relative to humeri of Neandertals and Early Upper Paleolithic (later Aurignacian and Gravettian) modern humans. On the basis of diaphyseal cross-sectional geometry, deltoid tuberosity morphology, and distal epiphyseal morphology, the specimen falls clearly and consistently with European early modern humans and not with Neandertals. Along with the other Vogelherd human remains, the Vogelherd humerus represents an unequivocal association between the Aurignacian and modern human morphology in Europe. *Am J Phys Anthropol* 112:251–273, 2000.

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Models of the cultural processes involved in the transition from the Middle to the Upper Paleolithic in Europe are based upon the temporal, typological, and technological relationships between Mousterian, early “transitional” (e.g., Châtelperronian, Uluzzian, Szeletian), and Aurignacian assemblages. The temporal and geographic pattern of the appearance of early Upper Paleolithic industries in Europe is a complex one, and has led to different interpretations of the cultural and populational dy-

namics involved (e.g., Straus, 1994 vs. Harrold, 1989; d’Errico et al., 1998). Reconstructing the population biological events surrounding the Middle-to-Upper Paleo-

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lithic transition and its connection with the appearance of modern humans in Europe, and the role of technological change or cultural diffusion in these events, is made difficult by a paucity of well-provenanced human fossils from early Upper Paleolithic contexts. Implicit in much of the discussion of the dynamics of modern human origins in this region is the assumption that the Aurignacian, from its very start, was made by fully modern humans. Unfortunately, diagnostic fossil remains associated with the earliest Aurignacian are rare, and the makers of the earliest Upper Paleolithic are not well-known (Gambier, 1997; Straus, 1997).

It is generally assumed that in Europe, Neandertals produced the Middle Paleolithic and so-called "transitional" industries¹ (Châtelperronian, Uluzzian, Lincombian, Szeletian, Bohunician), and that anatomically modern humans produced the Aurignacian and subsequent Upper Paleolithic industries (see Stringer et al., 1984; Gambier, 1989; Stringer, 1992; d'Errico et al., 1998). This assumption of direct hominid-lithic industry associations lies at the base of many discussions of the biological and cultural transitions that occurred in Europe between 40 and 30 Ky bp. This taxonomy-typology paradigm is based on the nearly exclusive association (at least in Europe if not in the Near East) of Neandertal fossils with Mousterian assemblages, and the recovery of modern human fossils associated with Aurignacian or Aurignacian-like assemblages from scores of sites in Eastern and Western Europe.

The recovery of Neandertal remains from the Aurignacian-like G₁ level at Vindija Cave (Croatia) (Wolpoff et al., 1981; Smith and Ahern, 1994; Karavanić, 1995; Karavanić and Smith, 1998), with direct dates of 28–29 Ky bp (Smith et al., 1999), presents a challenge to an assumed Aurignacian-modern human correlation, and calls into question the sagacity of assuming that contemporaneity of Châtelperronian and early

Aurignacian levels in Western Europe demonstrates a coexistence of Neandertals and early modern humans. However, the correlation of the Vindija G₁ hominids with the Aurignacian-type tools from that level (bone points, including one with a split base) is not universally accepted (see d'Errico et al., 1998). Miracle (1998) has raised the possibility that Vindija G₁ represents a Szeletian level, and most recently, Karavanić and Smith (1998) suggested that the assemblage from this level represents a regional early Upper Paleolithic variant rather than classic Aurignacian. Thus Vindija may not demonstrate an association between Neandertals and the Aurignacian *sensu stricto*.

In this light, the isolated humerus recovered from early Aurignacian levels at Vogelherdhöhle, near Stetten, Germany (Gieseler, 1937), is important for its potential to identify the morphological and taxonomic affinities of the makers of the earliest Aurignacian. The great robusticity and muscularity of the Vogelherd humerus has engendered speculations that it may represent a Neandertal (Gieseler, 1937) or an early modern human that retained Neandertal characteristics (Wolpoff, 1996). This latter possibility has been raised for the Aurignacian cranial material from the same site. Specifically, the Stetten 1 cranium has been argued to show distinct Neandertal features (Frayer et al., 1993), namely a retromolar space and a horizontal-oval mandibular foramen (see also Frayer, 1992).

In this paper we describe the isolated humerus from the early Aurignacian of Vogelherd and reassess its morphology and taxonomic affiliation.

THE VOGELHERD 3 HUMERUS

Background

Vogelherd cave is located in a hilly ridge on the east rim of the Lone River Valley (Lonetal), in southwestern Germany (Fig. 1). The cave's name comes from the local term for the hilly ridge itself, which rises approximately 18 m above the valley floor. Because it is located only about 1 km northwest of the small town of Stetten ob Lonetal, the site has also come to be known as Stetten.

¹Our choice of the term "transitional" is meant to reflect the communalities these industries share with earlier Mousterian and later Upper Paleolithic industries, and is not meant as a statement of the evolutionary relationships between Middle and Upper Paleolithic cultures in Europe.

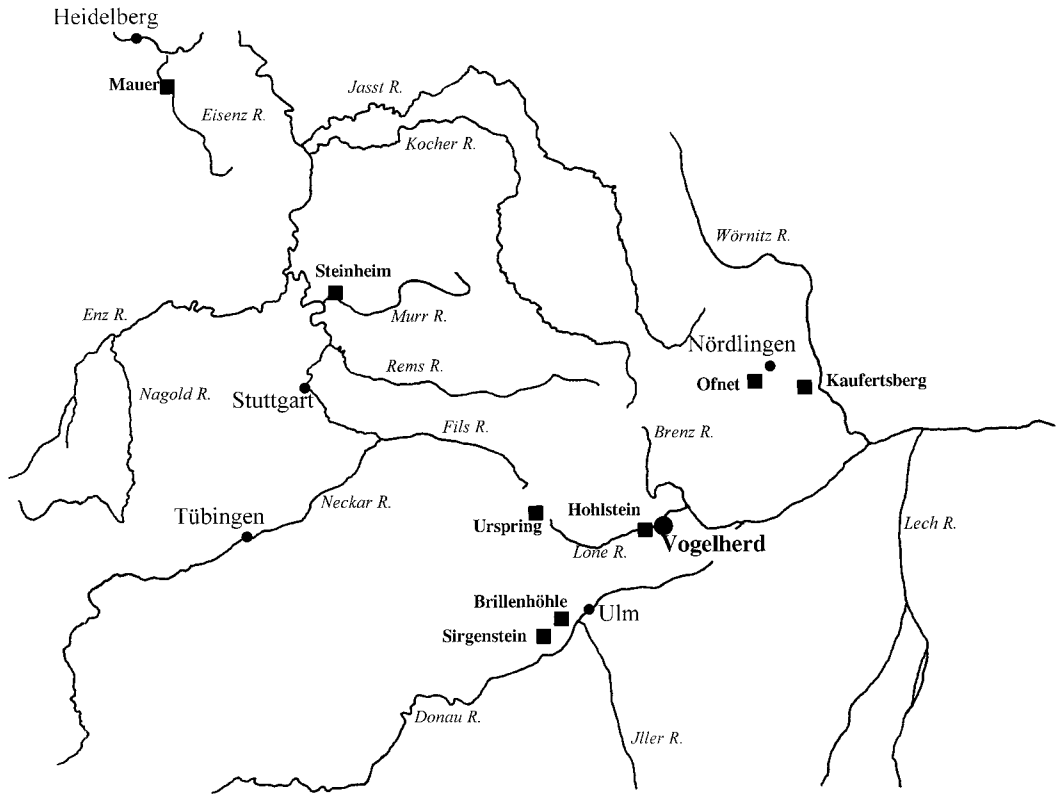


Fig. 1. Location of Vogelherd Cave ($48^{\circ} 34' \text{ N}$, $10^{\circ} 12' \text{ E}$) relative to major river drainages and nearby fossil hominid sites (redrawn from Gieseler, 1940).

The Vogelherd cave was discovered by an amateur natural historian in 1931 and was excavated from early July through late September of that year under the direction of Gustav Riek (Riek, 1932, 1934), from the Prehistoric Institute of the University of Tübingen. The internal portion of the cave is about 23 m in length and ranges between 3–6 m in breadth (Fig. 2). There are two main entrances, one facing south and the other facing southwest. Archaeological and other deposits also extend out onto the terraces in front of both entrances. The average depth of the deposits varies but generally falls between 2–4 m (Riek, 1934). Riek's excavations yielded a stratified series of cultural levels extending from the Acheulean to the Neolithic, as well as sterile layers of limestone debris. The most significant finds comprise lithics and bone tools, as well as several small animal and anthropomorphic figures carved from mammoth ivory, that are characteristic

of the Aurignacian (Riek, 1934; Hahn, 1977, 1983; Müller-Beck, 1983).

Riek identified three phases of the Aurignacian at Vogelherd, which he designated as the lower, middle, and upper Aurignacian. The "lower Aurignacian" was represented by only a few stone and two bone tools, and no animal carvings were recovered from this component (Riek, 1934). Subsequently, Müller-Beck (1983) noted that these tools were basically characteristic of the Mousterian rather than the Aurignacian and redesignated Riek's "lower Aurignacian" as late Mousterian. Riek's "middle Aurignacian" is now designated as horizon V and represents the early Aurignacian at the site, while the late Aurignacian is designated as horizon IV (Table 1). The typically Aurignacian tools and carvings derive from these two horizons.

Human skeletal elements from at least 3 adult individuals were recovered from Vo-

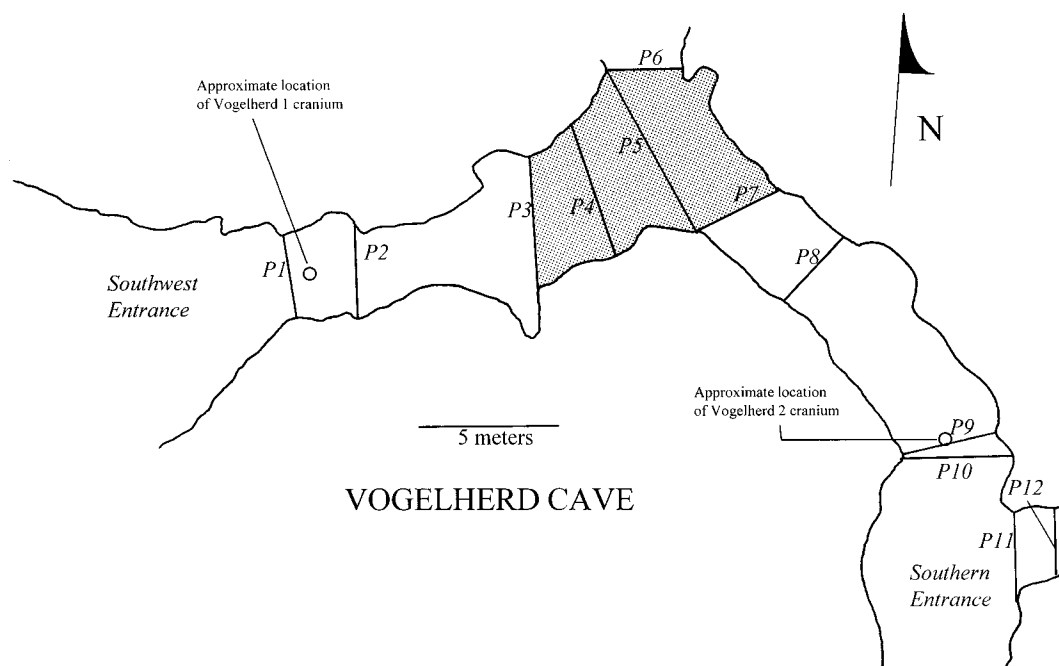


Fig. 2. Plan of Vogelherd Cave, showing the location of the profiles described by Riek (1932, 1934). The Vogelherd 1 cranium was recovered near the southwestern entrance of the cave, while the Vogelherd 2 cranium was found inside the southern entrance. The humerus was recovered from the central portion of the cave, between profiles 3 and 6 (stippled).

TABLE 1. Horizons/tool kit complements at Vogelherd Cave¹ from youngest (II) to oldest (IX)

Horizons	Tool tradition
II	Magdalenian
III	Magdalenian
Cranium V2 (top of layer IV)	
IV	Aurignacian
Skull V1 (top or bottom of layer V)	
V	Aurignacian
Humerus V3 (bottom of layer V)	
VI	Late Mousterian
VII	Mousterian
VIII	Micoqian
IX	Early Mousterian

¹ Adapted from Müller-Beck (1983).

gelherd (Table 1; Gieseler, 1937, 1940, 1971; Czarnetzki, 1980, 1983; Smith, 1984), and have generally been referred to as the Stetten remains. The first specimen, Vogelherd (Stetten) 1, consists of a modern human cranium (lacking most of the face) and a partial mandible (found 0.15 m east of the cranium and 0.33 m deeper) (Fig. 3). Both were found in a "Brandschicht" or burned layer at the position of profile 1 in front of the southwest

entrance (Riek, 1932, 1934). Two lumbar vertebrae were found 2–3 m east of the cranium in the same layer. The color of the vertebrae is identical to that of the skull, and the vertebrae were also attributed to Vogelherd 1 (Riek, 1932). The layer containing these remains is now designated as horizon V at Vogelherd and is considered to represent an early Aurignacian component (Hahn, 1983; Müller-Beck, 1983). There is some confusion in the literature concerning where in horizon V the human remains were found. Gieseler (1937, p. 42) reports that the cranium and burned layer were located between the "middle and upper Aurignacian," which would place it at the top of horizon V. However, Riek (1934, p. 40–41) clearly describes and illustrates Vogelherd 1 and the burned layer to lie at the base of this horizon.

The second individual, Vogelherd (Stetten) 2 (Fig. 3), was discovered at profile 9 just inside the south entrance of the cave and separated by the entire length of the cave from Vogelherd 1. According to Riek

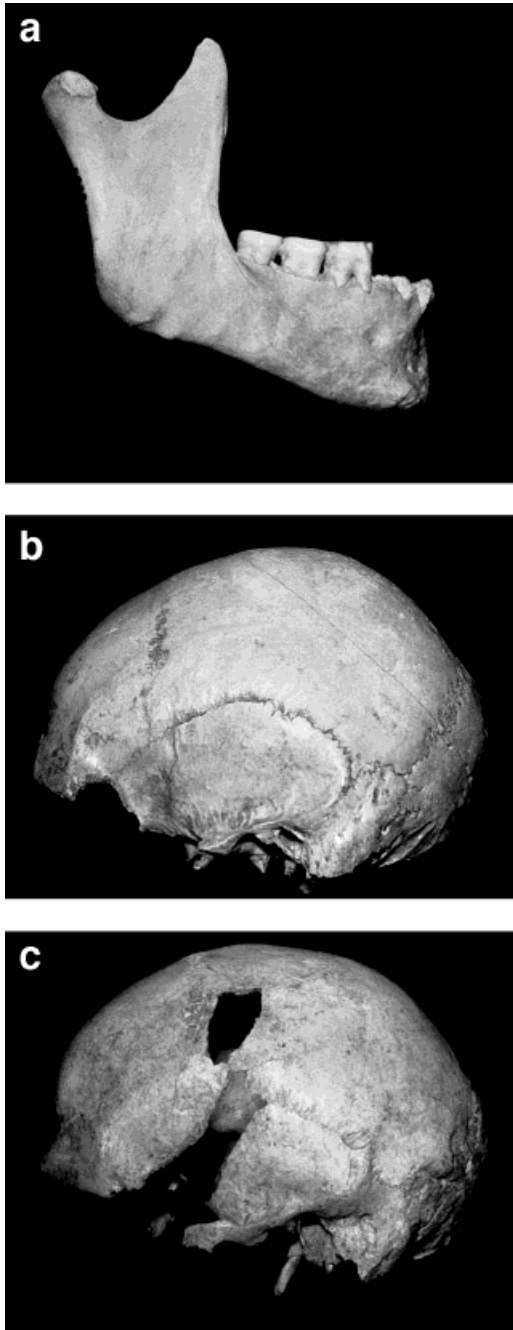


Fig. 3. Lateral views of the Vogelherd 1 mandible (a) and cranium (b) and the Vogelherd 2 cranium (c).

(1934), it was found at the top of the upper Aurignacian layer (now level IV), and there were noncultural layers deposited above it in this area of the cave (a layer of fine splin-

tered limestone colored yellow-white). While Riek (1934) pointed out that there was no intermingling of this limestone layer with the Aurignacian layer in this area, Gieseler (1937) believed that Vogelherd 2 might have been deposited by later Magdalenian peoples.

From a morphological standpoint, both Vogelherd crania unequivocally represent modern humans (Gieseler, 1937), albeit with some archaic features (Smith, 1984; Frayer et al., 1993). These finds were significant to German science during the 1930s, because they were the first relatively complete early Upper Paleolithic specimens from Germany and thus elevated Germany to the same level as France and Moravia (Czech Republic) in terms of remains of early modern Europeans (Gieseler, 1940). The skulls were particularly significant for Riek, as he believed they demonstrated complex ritual behavior, possibly trophy head taking, on the part of the Vogelherd Aurignacian people (Riek, 1934, p. 302–308).

The third individual from Vogelherd elicited no real interest from Riek. Vogelherd 3 consists of a robust right humerus, lacking its proximal end. According to Gieseler (1937, p. 43), this specimen derived from near the middle of the cave at the base of the “middle Aurignacian” (now early Aurignacian, horizon V). Furthermore, Gieseler (1937) stated that the specimen was excavated partly from this level and partly from the underlying sterile layer comprised of large, coarse pieces of limestone rubble (“grobstückiger Kalkschutt”). This would have to place the location of Vogelherd 3 somewhere between Riek’s profiles 3 and 6, because this is the portion of the site where the “middle Aurignacian” directly overlies such a level (Riek, 1934, p. 42–45). Such a location would be commensurate with Gieseler’s placement of the specimen near the center of the cave (Fig. 2). Also, according to Gieseler (1937, p. 43): “Riek assumes that, according to the profile, this humerus is probably somewhat older than the Stetten I skull.”

Gieseler was entrusted to describe the Vogelherd human remains, which he accomplished to some extent in the case of

TABLE 2. Comparison of levels and dates from Geißenklosterle and Vogelherd¹

Site	Horizon	Culture	C ¹⁴ date	Error	Climate
Vogelherd	IV	L. Aur.	30,730	750	Cool-dry
Vogelherd	V	E. Aur.	30,162	1,340	Cool-humid
Vogelherd	V	E. Aur.	31,900	1,100	Cool-humid
Geißenklosterle	2a	L. Aur.	30,625	796	Cool-dry
Geißenklosterle	2a	L. Aur.	31,525	770	Cool-dry
Geißenklosterle	2b	L. Aur.	31,070	750	Cool-dry
Geißenklosterle	2b	L. Aur.	31,870	1,000	Cool-dry
Geißenklosterle	2b	L. Aur.	32,680	470	Cool-dry
Geißenklosterle	2b	E. Aur.	33,700	825	Cool-humid
Geißenklosterle	3	E. Aur.	34,140	1,000	Cool-humid
Geißenklosterle	3?	E. Aur.	36,540	1,570	Cool-humid

¹ Aurignacian horizons at Geißenklosterle and Vogelherd, showing the cultural, temporal, and climatic correlations. C¹⁴ date and error given in radiocarbon years. Data taken from Müller-Beck (1983).

the skulls (Gieseler, 1937, 1940). However, his only comments regarding the morphology of the Vogelherd 3 humerus were to note that it is robust, with well-developed muscle insertions. Gieseler stated that these features suggest Vogelherd 3 might represent a Neandertal and that its stratigraphic position supports that possibility (1937, p. 43, 1940, p. 116). Gieseler never provided any additional assessment of this specimen.

Chronology

There are three radiocarbon dates reported from horizons IV ($30,730 \pm 750$) and V ($30,162 \pm 1,340$; $31,900 \pm 1,100$) at Vogelherd by Müller-Beck (1983), which in concert with radiocarbon dates from several other significant German sites (principally Geißenklosterle) indicate that the Aurignacian probably began earlier in Germany than in France (Table 2). Hahn (1983) reported that the Aurignacian at Geißenklosterle occurs in horizons 3 and 2a–2d. Climatic reconstruction suggests that Vogelherd horizon IV and Geißenklosterle horizons 2a and 2b correspond to cold-dry periods, while Vogelherd horizon V and Geißenklosterle horizons 2d and 3 correspond to cold-humid periods (see Table 2). The ¹⁴C determinations from Vogelherd horizon V provide a minimum age for the specimen, since it was recovered from the base of this horizon. The humid climatic conditions suggest a Würm II/III interstadial age (Les Cottés II/III or Hengelo II temperate oscillation), which would be consistent with dates from the early Aurignacian levels at Geißenklosterle. Radiocarbon dates from

the base of Geißenklosterle (horizon 3) are reported to be 34,000–36,500 years bp (Hahn, 1983). If this corresponds to Vogelherd horizon V (the earliest level of Aurignacian at Vogelherd), then the base of horizon V may even predate 34,000–36,500 radiocarbon years bp.

Given that the Vogelherd 3 humerus was found at the base of horizon V, it seems most likely that it derives from the end of the Würm II/III interstadial. This makes the Vogelherd 3 humerus one of the earliest Aurignacian fossils yet recovered, and places it in the critical time period spanning the appearance of modern people and the disappearance of Neandertals in this part of Europe.

Preservation

The specimen is a largely intact right humerus, missing the head proximally and portions of the capitulum and medial epicondyle distally (Fig. 4). Proximally the bone is preserved to the region of the surgical neck, such that the entire articular surface of the head and all but the inferior portions of the greater and lesser tubercles are missing. The maximum preserved length of the specimen is 305 mm. Medially the metaphysis is broken just inferior of the inferomedial margin of the head articular surface.

The shaft is well-preserved, except that two large superoinferiorly oriented cracks are present on the proximal end. The medial surface of the shaft has a fracture extending roughly halfway (152 mm) down the specimen, while the lateral surface is split to the region of the deltoid tuberosity (75 mm from



Fig. 4. The Vogelherd 3 humerus (from left to right) in anterior, medial, posterior, and lateral views. One-half natural size.

the proximal margin of the preserved diaphysis). Both cracks obtain a maximum width of 1 mm and exhibit inward compression of the bone margins, and thus represent post-mortem damage to the specimen. Otherwise, preservation of the surface morphology of Vogelherd 3 is excellent, and the apparent degree of permineralization of the specimen is relatively slight.

The distal epiphysis lacks the distal and distal-medial portions of the medial epicondyle; the lateral, inferior, and most of the superior portions of the capitular articular surface; and the anteromedial portion of the lateral epicondyle (the attachment surface for the common extensor tendon). The capitulum and adjacent lateral epicondyle have been reconstructed in wax. The medial trochlear articular margin exhibits some abrasion along its anterior portion.

Estimation of length

Maximum length estimates for Vogelherd 3 were obtained by linear regression, using various predictor variables and reference samples. Estimation of humeral length is most accurate when the predictor variable incorporates most of the length of the bone and has a high correlation coefficient with length. We used the distance between the base of the lesser tubercle and the distal-most point on the trochlea (hereafter "tubercle-trochlea length") as a predictor of maximum humeral length. The regression was conducted on a pooled-sex sample of 37 Neolithic humeri from southwestern Germany curated at the University of Tübingen (Smith, unpublished data). By simple linear regression analysis (Model I LSA), maximum length can be predicted as:

$$1.13 * (\text{tubercle-trochlea length}) \\ - 0.74; r = 0.98.$$

The lesser tubercle-distal trochlear length of Vogelherd 3 (299.9 mm) produces an estimated maximum length of 338.1 mm.

Additionally, we used regression of humeral *articular* length (from the most proximal point on the articular surface of the head to the most distal point on the lateral trochlear margin, parallel to the shaft axis) and the distance from the distal-most point of the deltoid tuberosity to the most distal point on the lateral trochlear margin ("DT-trochlea length"). Regressions were conducted on three mixed-sex samples: Neandertals ($n = 11$); early Upper Paleolithic modern humans ($n = 17$); recent (Holocene); and fossil modern humans combined ($n = 238$) (details of sample composition can be found in Churchill, 1994). In all samples, side (right vs. left) was selected at random. The ratio of DT-trochlea length to humeral length is somewhat variable, and thus DT-trochlea length is a less effective predictor of humeral length than is tubercle-trochlea length. The resulting prediction formulae for humeral articular length are as follows:

Recent and fossil modern humans

$$(n = 238) 1.62 * (\text{DT-trochlea length}) \\ + 69.53; r = 0.90$$

Neandertals ($n = 11$) 1.56 *

$$(\text{DT-trochlea length}) + 79.95; r = 0.78$$

Early Upper Paleolithic ($n = 17$)

$$1.88 * (\text{DT-trochlea length}) + 31.61; \\ r = 0.91$$

The DT-trochlea length of Vogelherd 3 (163 mm) produces articular length estimates of 334.4 mm, 334.8 mm, and 337.9 mm. based on the total, Neandertal, and Early Upper Paleolithic samples, respectively. Articular length is usually about 3–6 mm less than maximum length; thus, these estimates are roughly concordant with the estimate from tubercle-trochlea length. Given that tubercle-trochlea length is a better predictor of bone length, we take 338 mm as the best

estimate of the maximum length of this specimen.

Sex of Vogelherd 3

Table 3 presents select measurements of the Vogelherd 3 humerus, as well as means for samples of Neandertal and early Upper Paleolithic males and females (see Table 4 for sample composition). Based on size, robusticity, and muscular rugosity, we feel that the Vogelherd 3 humerus represents that of a male. This conclusion is supported by consideration of two traits (minimum shaft circumference and distal articular breadth) that Trinkaus (1980) found useful in separating male from female Neandertal humeri. Minimum shaft circumference is plotted against humeral maximum length for fossil and combined fossil/recent human samples (data from Churchill, 1994) in Figure 5, while similar plots of distal articular breadth on epicondylar breadth are presented in Figure 6. In all cases, Vogelherd 3 falls among male data points and generally outside the range of female values. Accordingly, all subsequent comparisons of Vogelherd 3 to Neandertals and early Upper Paleolithic fossils will be restricted to specimens considered to represent males.

Morphology

The Vogelherd 3 humerus is heavily muscle-marked. Rugosity is pronounced in the insertion sites for *Mm. pectoralis major*, *latissimus dorsi*, *teres major*, and *deltoideus*, and in the origination areas of *Mm. triceps (lateralis)*, *brachioradialis*, and *extensor carpi radialis longus*. The most prominent feature on the proximal shaft is the enlargement of the *M. pectoralis major* insertion area (Fig. 7). The attachment area is very rugose and is present as a raised plateau roughly 50.6 mm long, with distinct margins medially and laterally. Distal of the plateau an area of rugosity extends an additional 43.5 mm distally, likely representing the distal fibers of the muscle. The maximum transverse breadth of the insertion scar (13.1 mm) is more than two standard deviations above the Neandertal male mean (Table 3) and more than seven standard

TABLE 3. Selected right humeral measurements of Vogelherd 3, Neandertals, and early Upper Paleolithic modern humans¹

	Neandertal females mean ± SD (n)	Neandertal males mean ± SD (n)	Vogelherd	Up. Paleo. males mean ± SD (n)	Up. Paleo. females mean ± SD (n)
Maximum length (M-1)	298.6 ± 20.6 (4)	313.1 ± 12.9 (8)	(338)	346.3 ± 24.2 (10)	320.3 ± 9.1 (3)
Deltoid tuberosity circumference ¹	63.1 ± 7.6 (4)	70.3 ± 2.7 (7)*	83.5	75.8 ± 7.8 (8)	70.0 (1)
Deltoid tuberosity width ²	9.3 ± 1.8 (4)*	11.3 ± 2.3 (7)*	23.7	19.1 ± 3.7 (8)	15.6 (1)
Pectoralis major breadth ³	6.2 ± 0.4 (3)*	9.7 ± 1.5 (7)	13.1	6.5 ± 0.9 (8)**	4.8 ± 2.4 (3)
Midshaft maximum diameter (M-5)	21.5 ± 2.1 (6)	25.3 ± 1.0 (8)	25.7	24.7 ± 3.7 (9)	21.2 ± 1.7 (3)
Midshaft minimum diameter (M-6)	15.7 ± 2.0 (6)	18.6 ± 1.7 (8)	19.5	19.2 ± 2.1 (9)	16.6 ± 1.2 (3)
Minimum circumference (M-7)	60.0 ± 4.8 (4)	67.9 ± 3.7 (7)	68.5	67.4 ± 5.9 (11)	61.2 ± 2.8 (3)
Epicondylar breadth (M-4)	61.8 ± 1.9 (2)	64.4 ± 2.2 (6)	(66)	63.2 ± 4.2 (7)	
Distal articular breadth (M-12a)	41.5 ± 1.7 (3)	45.0 ± 2.2 (10)	(47)	44.5 ± 3.5 (10)	41.6 ± 1.4 (3)
Trochlear breadth (M-11)	21.2 ± 2.1 (6)	22.7 ± 3.0 (10)	24.0	21.5 ± 2.2 (9)	19.0 ± 2.1 (2)
Medial trochlear depth ⁴	23.2 ± 2.0 (4)	25.7 ± 3.1 (8)	(27.5)	28.3 ± 2.4 (8)	24.2 ± 1.9 (2)
Mid-trochlear depth ⁴	14.5 ± 1.1 (6)*	16.0 ± 0.8 (10)*	18.2	19.4 ± 2.1 (9)	16.8 ± 1.3 (2)
Lateral trochlear depth ⁴	18.0 ± 1.7 (4)	19.7 ± 1.5 (7)	21.6	21.1 ± 1.7 (7)	18.7 ± 1.3 (2)
Olecranon fossa breadth (M-14)	27.6 ± 1.8 (6)	28.8 ± 1.4 (9)	25.9	26.0 ± 3.1 (9)	25.8 ± 0.6 (2)
Olecranon fossa height ⁵	20.2 ± 1.9 (5)	20.3 ± 1.3 (6)	19.4	19.9 ± 1.7 (9)	19.6 ± 0.1 (2)
Distodorsal medial pillar breadth ⁶	7.8 ± 2.7 (4)*	9.8 ± 1.4 (6)	12.2	11.6 ± 1.9 (7)	8.0 ± 0.5 (2)
Distodorsal lateral pillar breadth ⁶	14.8 ± 0.6 (3)*	17.3 ± 1.9 (7)	20.8	18.4 ± 2.1 (7)	17.4 ± 0.3 (2)

¹ All measurements in millimeters. Martin numbers (M-no.: Martin, 1928) provided where appropriate. Composition of comparative samples is provided in Table 5. Test of single observation against sample means based on modified *t*-test (Sokal and Rohlf, 1981, p. 231).

² Taken at 5/12 maximum length following Endo (1971); width taken between the apices of the anterior and posterior crests.

³ Maximum transverse breadth of the *M. pectoralis major* tendon insertion area.

⁴ Anteroposterior diameter of the medial trochlear margin, mid-trochlea at the narrowest point, and lateral trochlear margin.

⁵ Maximum superoinferior diameter of the olecranon fossa.

⁶ Diameter of pillar taken at the midpoint of the adjacent olecranon fossa margin.

* Vogelherd 3 significantly different from sample mean at $P \leq 0.05$.

** Vogelherd 3 significantly different from sample mean at $P \leq 0.001$.

deviations above the early Upper Paleolithic male mean. The *M. pectoralis major* insertion area is separated from the intertubercular groove by a small sulcus medially, and from the attachment area of *M. deltoideus* by a raised ridge posteriorly. Distinct crests can also be seen from *Mm. latissimus dorsi* and *teres major* on the medial side of the intertubercular sulcus.

The muscularity of this individual is further indicated by the relatively great width of the intertubercular sulcus, which measures 8.9 mm transversely at its proximal end, suggesting a hypertrophied tendon for the long head of *M. biceps brachii*. Additionally, there is a raised tubercle on the posterior proximal surface of the diaphysis, sug-

gesting some hypertrophy of the lateral head of *M. triceps brachii*.

Another striking feature of Vogelherd 3 overall is the development of the deltoid tuberosity (Fig. 4), which forms a large plateau bounded by a distinct raised and rugose ridge posteriorly. Anteriorly, the margin of the muscle scar does not project from the subperiosteal surface of the diaphysis, and were it not for an expanse of rugose bone extending to the middle of the anterior surface of the diaphysis, the true width of the muscle insertion would be indiscernible. The inflated size of the deltoid tuberosity is evident in part in its great circumference (taken at 5/12 maximum length) and width (transverse distance between the apices of

TABLE 4. *Fossil specimens*¹

	Cultural association
Neandertals	
Males	
La Chapelle 1	Charentian Mousterian (Quina)
La Ferrassie 1	Charentian Mousterian (Ferrassie)
Kebara 2	Phase 3 (Tabun B) Mousterian
Krapina 169, 170, 174 ²	Mousterian
Neandertal 1	No associated industry
Regourdou 1 ³	Charentian Mousterian (Quina)
Shanidar 3 and 4 ⁴	"Zagros" Mousterian
Spy 2	Mousterian
Females	
Krapina 166	Mousterian
La Ferrassie 2	Charentian Mousterian (Ferrassie)
La Quina 5	Charentian Mousterian (Quina)
Lezetxiki 1	"Pre-Mousterian"
Shanidar 6 ⁴	"Zagros" Mousterian
Spy 1	Mousterian
Tabun C1	Phase 2 (Tabun C) Mousterian
Early Upper Paleolithic	
Males	
Arene Candide 1 ⁵	Late Gravettian/early Epigravettian
Barma Grande 2, 5	Late Aurignacian/Gravettian
Baoussou da Torre 2	Gravettian?
Cro-Magnon 1, 3	Late Aurignacian
Dolní Věstonice 13, 14, 16	Eastern Gravettian (Pavlovian)
Grotte des Enfants 4	Gravettian
Paviland 1	British early Upper Palaeolithic
Pavlov 1	Eastern Gravettian (Pavlovian)
Predmosti 3, 9, 14 ⁶	Eastern Gravettian (Pavlovian)
Females	
Abri Pataud 5 ⁷	Proto-Magdalenian
Cro-Magnon 2	Late Aurignacian
Dolní Věstonice 3 ⁸	Eastern Gravettian (Pavlovian)
Paglicci 25	Gravettian
Predmosti 4, 10	Eastern Gravettian (Pavlovian)

¹ Dates and/or geological ages, along with references for original descriptions and cultural context, can be found in Churchill (1994).

² Sex determination following Trinkaus (1980).

³ Sex is indeterminate, considered as male in this study.

⁴ Data from Trinkaus (1983) (Shanidar 4 and 6).

⁵ Subadult (mid- to late teens at death).

⁶ Data from Matiegka (1938).

⁷ Sex is indeterminate, considered as female in this study.

⁸ Data from Trinkaus and Jelinek (1997).

the anterior and posterior crests, taken at 5/12 maximum length), which are significantly larger than the means observed in Neandertals, and which are on the high end of the ranges observed in early Upper Pa-

leolithic males (Table 3). The deltoid tuberosity exhibits three crests, the lateral two being very pronounced (Fig. 8). Despite the large size of the deltoid tuberosity, there is no sulcus evident between the anterior margin of the tuberosity and the diaphysis, as can be seen in some Neandertals and some modern humans (Trinkaus, 1983).

As in all Neandertals and anatomically modern humans, the distal shaft is triangular in section, but the lateral supracondylar margin is very well-developed and shows a well-developed attachment area for *M. extensor carpi radialis longus*. Proximal of the lateral supracondylar ridge, a moderately well-developed ridge for *M. brachioradialis* curves slightly anteromedially and onto the anterior supracondylar surface.

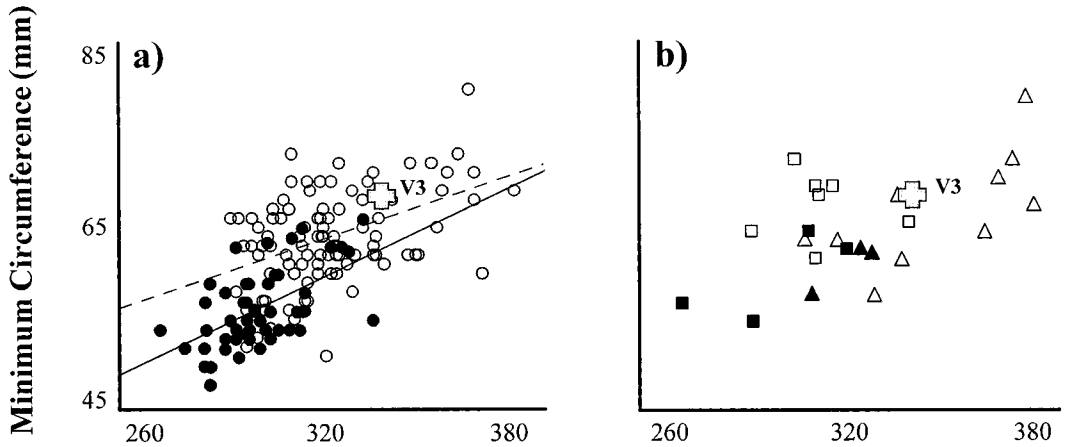
Neither of the epicondyles are preserved in Vogelherd 3, and the lateral epicondyle and capitulum have been reconstructed in wax. The superior edge of the medial epicondyle is preserved, and that along with the reconstruction of the lateral epicondyle allows for a reasonable estimate of epicondylar breadth (66 mm). On the anterior surface of the distal epiphysis, the *fossa coronoideus* is deeply excavated, and lateral to it the *fossa radialis* is also clearly visible. The septum between the coronoid and olecranon fossae is 1–2 mm thick and lacks perforations. The olecranon fossa is large and deeply excavated, with a maximum depth of 12.8 mm.

The trochlea possesses a distinct crest along its lateral margin separating it from the capitulum. The medial trochlear ridge has been abraded along the medial surface of the ridge as well as along the ridge rim. The majority of the capitulum is missing, but the wax reconstruction allows for a very crude estimation of distal articular breadth of 46–47 mm, with a maximum anatomically justifiable estimate of 48 mm.

COMPARISON OF VOGELHERD 3 WITH NEANDERTAL AND EARLY MODERN HUMAN HUMERI

Materials and methods

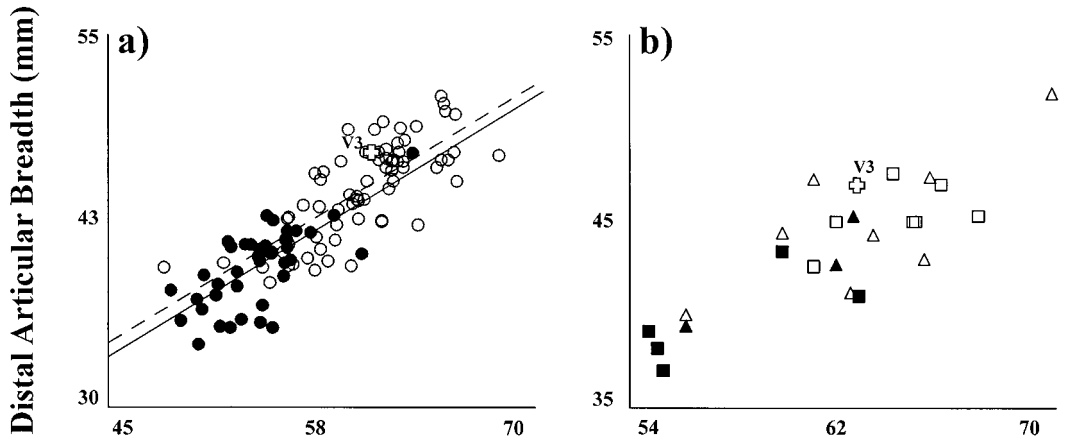
A number of characteristics have been argued to distinguish Neandertal humeri from those of modern humans. Perhaps the most



Humeral Maximum Length (mm)

Fig. 5. Humeral minimum shaft circumference on maximum length for (a) combined recent human and fossil samples and (b) fossil samples. Females are represented by solid symbols (and the solid regression line), and males by open symbols (and dashed regression line). Recent human data are from Churchill (1994).

Left-side values were used for four Neandertals (Krapina 166, Shanidar 6, Spy 2, and Tabun C1) and four early Upper Paleolithic modern humans (Barma Grande 5, Cro-Magnon 2, Grotte des Enfants 4, and Paglicci 25).



Epicondylar Breadth (mm)

Fig. 6. Humeral distal articular breadth on epicondylar breadth for (a) combined recent human and fossil samples and (b) fossil samples. Females are represented by solid symbols (and the solid regression line), and males by open symbols (and dashed regression line). Recent human data are from Churchill (1994).

commonly noted suite of features involves the morphology of the mid-diaphysis and deltoid tuberosity. Neandertals and other archaic *Homo* are characterized by absolutely and relatively narrow deltoid tuberosities (Weidenreich, 1941; Endo, 1971;

Thoma, 1975; Hambücker, 1993; Churchill, 1994; Carretero et al., 1997) with two rather than three crests (Endo, 1971; Thoma, 1975; Vandermeersch, 1981; but see Hambücker, 1993), and a humeral midshaft that is relatively mediolaterally compressed (platy-



Fig. 7. Detail of the *M. pectoralis major* insertion area of Vogelherd 3 (left), seen here next to a German Neolithic male (right), also with a large muscle insertion area. The anterior and middle crests of the deltoid tuberosity are also visible in this perspective. One-half natural size.

brachic: Trinkaus, 1983; Hambücker, 1993; Carretero et al., 1997). Neandertal humeri also tend to have low torsion angles (Churchill, 1994; Carretero et al., 1997), a feature that has been argued to account for their narrow deltoid tuberosities (Carretero et al., 1997; but see Discussion, which follows). In addition, Neandertal humeral diaphyses tend to be robust (i.e., with thick cortical bone relative to bone length: Trinkaus, 1983; Churchill, 1994; but see Hambücker, 1993, 1995) and relatively stenotic (i.e., having narrow medullary spaces relative to shaft cross-sectional area²: Ruff et al., 1993; Churchill, 1994). While overall upper limb (or for that matter, postcranial)

²The term "stenosis," referring to narrowing of a canal, is widely used in medicine and thus carries a connotation of pathology or abnormality. The term has also been applied to relative reduction of the medullary space in healthy long bones (e.g., Garn et al., 1968; Kennedy, 1985), and it is in this non-clinical sense that we use the term here.



Fig. 8. Detail of the *M. deltoideus* insertion area, showing the middle and posterior crests. One-half natural size.

robusticity is characteristic of Neandertals, it should be borne in mind that neither absolute nor relative bone strength serves as a reliable feature for differentiating archaic from modern *Homo* (Pearson and Grine, 1996; Churchill et al., 1996). Proximally, Neandertal humeri are characterized by large heads that are transversely wider than tall (superoinferiorly) (Carretero et al., 1997), expanded lesser tubercles (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997), and large *M. pectoralis major* insertion scars (Trinkaus, 1983). Distally, Neandertal humeri tend to have enlarged epiphyses with large articular surfaces and large olecranon fossae (Trinkaus, 1983; Hambücker, 1993). Carretero et al. (1997) did not find that the relative size of the distal articular surface distinguished Neandertals from modern humans, but they did note a difference in the morphology of the olecranon fossa, with Neandertal humeri tending to have narrower medial and lateral distal pillars (a reflection of their larger

olecranon fossae) and medial pillars that are narrow relative to the lateral ones.

The proximal epiphysis of the Vogelherd 3 humerus is insufficiently preserved to allow for comparison of its morphology with those of other hominid groups. We thus examined measures of the shape of the Vogelherd 3 diaphysis and distal epiphysis relative to those of Neandertal and early modern European males. Shape indices were derived from measurements defined in Table 3, or from geometric properties of diaphyseal cross sections. Diaphyseal cross sections were reconstructed noninvasively from external contour molds and biplanar radiographs, as detailed elsewhere (Churchill, 1994). Reconstructed sections were manually digitized and analyzed with an interactive PC-version (Eschman, 1990) of SLICE (Nagurka and Hayes, 1980). For each cross section, we were able to determine the total cross-sectional area (TA), the cortical area (CA), medullary cavity area (MA), second moments of inertia in the anteroposterior and mediolateral planes (I_{AP} and I_{ML}), and the polar moment of inertia (J). When standardized by powers of humeral length (thus producing measures of "robusticity" sensu Ruff et al., 1993), these values provide a measure of the contribution of bony architecture to the resistance of various biomechanical loads at a particular diaphyseal level (see footnote to Table 7).

Data were collected from right humeri only, except for measurements of the distal pillars, which incorporate values from three Neandertal left humeri. We felt this to be a reasonable way to increase the Neandertal sample n given that upper limb epiphyses tend to exhibit minimal asymmetry (usually less than 2%), even in individuals with extreme diaphyseal asymmetry (Trinkaus et al., 1994; Churchill and Formicola, 1997). We conducted univariate tests of difference between a single variate (Vogelherd 3) and sample means (either Neandertals or early modern humans), as well as canonical variates analysis (CVA) on raw and "log-shape" variables (Darroch and Mosimann, 1985). When used as a discriminant tool, canonical variates analysis identifies the linear combination of variables that best differentiate between groups (Lindsey et al., 1985), and

thus is well-suited to questions of taxonomic or morphological affinities of isolated fossil remains (e.g., see Churchill et al., 1996). In order to maximize fossil samples, we conducted the CVA on a subset of variables from the distal two thirds of the humerus (the area of the head and neck is more prone to taphonomic destruction and is less well-represented in the fossil record). These variables are defined in Tables 3 and 6 and include deltoid tuberosity width, midshaft maximum and minimum diameters, midshaft cross-sectional cortical and medullary areas, distodorsal medial and lateral pillar breadths, epicondylar breadth, and distal articular breadth. The square roots of the cortical and medullary areas were entered into the CVA to keep all of the variables in the same measurement units. Some of the within- and between-group variance in humeral morphology may be related to variance in size, and thus size variation may obscure relevant similarities and differences in shape between groups. Accordingly, we also conducted the CVA on "log-shape" variables (Darroch and Mosimann, 1985): the logged ratio of each variable to the geometric mean of all the variables. By reducing the effects of size differences between specimens, this method has been shown to improve the phylogenetic signal in comparative data, and has several advantages over regression-based methods of size standardization (see Falsetti et al., 1993).

The Neandertal sample was composed of 11 males (Table 4) ranging in geologic age from the Last Interglacial to the Late Interpleniglacial. Geographically these specimens span the area from the Zagros to Northern Europe, but all are associated with Middle Paleolithic (Mousterian) assemblages. Early modern humans were represented by 15 Early Upper Paleolithic males (Table 4) from the earlier part of the Upper Pleniglacial (all predating the Last Glacial Maximum). Most of these specimens derive from Central European or Italian Gravettian contexts. Further detail on the geochronologic and cultural associations of these specimens can be found in Churchill (1994). All data were collected by the authors unless otherwise indicated in Table 4.

TABLE 5. Humeral diaphyseal and distal epiphyseal shape indices: right humeri, males only

	Neandertals mean \pm SD (n)	Vogelherd 3	Early Upper Paleolithic mean \pm SD (n)
Pectoralis major index ¹	38.5 \pm 5.9 (7)	51.0	26.8 \pm 5.7 (8)*
Pectoralis major breadth index ²	3.1 \pm 0.5 (7)	3.9	1.9 \pm 0.3 (8)*
Mid-proximal % CA ³	71.1 \pm 7.9 (7)*	45.6	60.9 \pm 6.3 (7)
Deltoid index ⁴	16.1 \pm 3.5 (7)*	28.4	25.0 \pm 2.5 (8)
Deltoid breadth index ⁵	3.6 \pm 0.7 (7)*	7.1	5.7 \pm 0.9 (7)
Midshaft index ⁶	73.5 \pm 6.3 (8)	75.9	78.2 \pm 4.5 (9)
Midshaft % CA ⁷	77.6 \pm 4.5 (7)*	54.1	63.5 \pm 5.7 (5)
Mid-distal % CA ⁸	80.9 \pm 6.7 (6)	75.1	71.3 \pm 7.4 (8)
Olecranon index ⁹	44.2 \pm 1.6 (5)	41.1	43.1 \pm 5.0 (6)
Pillar index ^{10,15}	56.1 \pm 6.6 (10)	58.7	63.1 \pm 8.7 (7)
Medial pillar index ^{11,15}	14.7 \pm 1.4 (8)*	19.4	18.6 \pm 2.2 (5)
Lateral pillar index ¹²	26.5 \pm 1.8 (8)*	33.0	30.1 \pm 2.0 (5)
Distal articular index ¹³	70.5 \pm 2.4 (6)	74.6	71.2 \pm 4.3 (7)
Distal breadth index ¹⁴	14.9 \pm 0.5 (7)	13.9	13.0 \pm 0.7 (10)

¹ Pectoralis major index: 100 * pectoralis major breadth/midshaft maximum diameter.

² Pectoralis major breadth index: 100 * pectoralis major breadth/humeral maximum length.

³ Mid-proximal %CA: 100 * diaphyseal cross-sectional cortical area/total area, taken at 65% of articular length as measured from the distal end.

⁴ Deltoid index: 100 * deltoid tuberosity width/deltoid tuberosity circumference.

⁵ Deltoid breadth index: 100 * deltoid tuberosity width/humeral maximum length.

⁶ Midshaft index: 100 * midshaft minimum diameter/midshaft maximum diameter.

⁷ Midshaft %CA: 100 * midshaft cross-sectional cortical area/total area.

⁸ Mid-distal %CA: 100 * diaphyseal cross-sectional cortical area/total area, taken at 35% of articular length as measured from the distal end.

⁹ Olecranon index: 100 * olecranon fossa ML diameter/epicondylar breadth.

¹⁰ Pillar index: 100 * medial pillar breadth/lateral pillar breadth.

¹¹ Medial pillar index: 100 * medial pillar breadth/epicondylar breadth.

¹² Lateral pillar index: 100 * lateral pillar breadth/epicondylar breadth.

¹³ Distal articular index: 100 * distal articular breadth/epicondylar breadth.

¹⁴ Distal breadth index: 100 * distal articular breadth/humeral maximum length.

¹⁵ Includes left humeral data from Krapina 160 and 161 and Kebara 2 (see text).

* Vogelherd 3 significantly different from sample mean at $P \leq 0.05$. Test of single observation against sample means based on modified t -test (Sokal and Rohlf, 1981, p. 231). Composition of comparative samples is provided in Table 4. See Tables 3 and 6 for definitions of measurements used to calculate indices.

Results

The Vogelherd 3 humerus differed from the early Upper Paleolithic sample mean in only 2 of 14 shape indices examined, yet differed from the Neandertal sample mean in 6 of these indices (Table 5). The only feature that separates Vogelherd 3 from the early modern males is the relative breadth of the insertion scar for *M. pectoralis major*. The insertion area for this muscle is considerably wider in Vogelherd 3 than in either of the fossil groups, but this difference only reaches statistical significance (at $\alpha = 0.05$) for the comparison with the early modern males (note that with respect to the pectoralis major index (Table 5) that Vogelherd 3 is more than 2 standard deviations away from the Neandertal mean, with an associated t -test P -value = 0.08). Based on the absolute and relative size of the *Mm. pectoralis major* and *deltoideus* insertion scars (Tables 3 and 5), it is clear that Vogelherd 3 had a marked degree of upper limb musculature.

The Vogelherd 3 humerus differs from the Neandertal sample means in four morphological features: the relative width and number of crests of the deltoid tuberosity, the degree of medullary stenosis in the proximal half of the diaphysis, and in the form of the distal pillars that abut the olecranon fossa. The deltoid tuberosity (measured from the apices of the anterior and posterior crests at 5/12 humeral length) is considerably wider in Vogelherd 3 than in the male Neandertals, whether considered in absolute terms (Table 3) or relative to diaphyseal circumference or humeral length (Table 5, Fig. 9). While the deltoid tuberosity in Vogelherd 3 is also wide relative to that of early modern human males (Tables 3 and 5), it does not differ significantly from the mean raw or index values obtained for that sample. The relative width of the deltoid tuberosity of Vogelherd 3 is fully modern (or even "hypermodern").

The number of rugose crests on the deltoid tuberosity of Vogelherd 3 adds to the

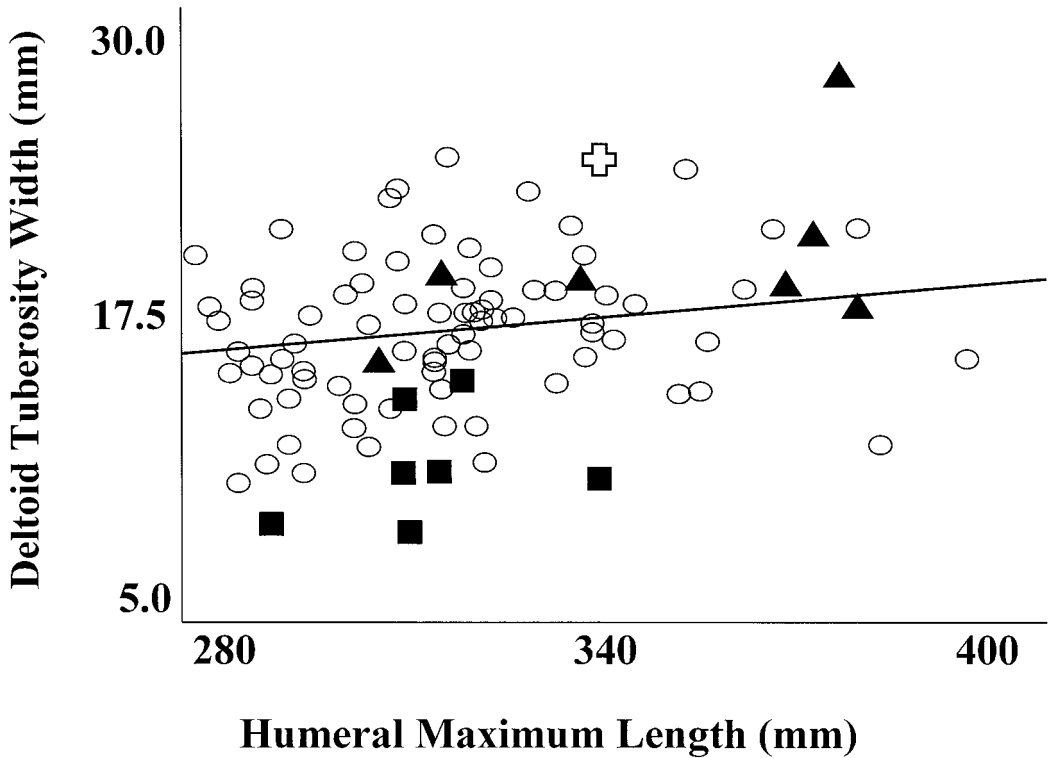


Fig. 9. Deltoid tuberosity width on humeral maximum length in three groups of males: Neandertals (solid squares, nonsignificant regression, $r = 0.290$, $P > 0.50$); Early Upper Paleolithic (solid triangles, nonsignificant regression, $r = 0.524$, $P = 0.120$); and recent modern humans (open circles, solid LS regression line $y = 8.831 + 0.025x$, $r = 0.193$, $P = 0.087$). Recent human data are from Churchill (1994).

impression of modern morphology. Neandertals are generally considered to be characterized by tuberosities with two rather than three crests (Endo, 1971; Thoma, 1975; Vandermeersch, 1981), but it should be noted that Hambücker (1993) found the number of crests to be highly variable in modern populations, and thus of dubious taxonomic utility. Still, the presence of three crests on Vogelherd 3's deltoid tuberosity supports the seeming modern affinities of this specimen.

The mid-diaphysis of Vogelherd 3 is not strongly platybrachic, and its intermediate value between the Neandertal and early modern male means is not statistically different from either group. Vogelherd 3 does differ from Neandertals, however, in the internal morphology of the proximal humeral shaft. Vogelherd 3 has an absolutely and relatively large medullary cavity (Tables 5 and 6). Percent cortical area (CA as a per-

centage of total cross-sectional subperiosteal area) serves as a direct measure of medullary stenosis. At midshaft, Vogelherd 3 has a percent cortical area value more than five standard deviations below the Neandertal mean, and is even well below (1.6 standard deviations) the Upper Paleolithic male mean (Fig. 10). This "nonstenotic" humeral morphology is characteristic of Upper Paleolithic and recent (Holocene) modern humans (but not Middle Stone Age and Middle Paleolithic associated modern humans from Africa and the Levant: Churchill, 1994; Pfeiffer and Zehr, 1996), and in this regard Vogelherd 3 is again distinguished from Neandertal males and appears "hypermodern" in form. In the mid-distal humeral shaft, Vogelherd 3 is again less stenotic than the Neandertal mean (Table 5), but not significantly so.

Distally, the olecranon fossa of Vogelherd 3 is relatively small (Tables 3 and 5), com-

TABLE 6. Unstandardized humeral cross-sectional properties: right humeri, males only¹

	Neandertals mean ± SD (n = 6)	Vogelherd 3	Early Upper Paleolithic mean ± SD (n = 8)
Mid-distal			
Total area ²	330.8 ± 22.4	377.2	365.1 ± 58.1
Cortical area ³	267.0 ± 22.8	283.2	262.4 ± 62.0
Medullary area ⁴	63.8 ± 24.0	94.0	91.7 ± 13.5
A-P 2nd moment ⁵	9,554.3 ± 1,412.1	11,128.2	11,845.8 ± 4,653.7
M-L 2nd moment ⁶	7,536.8 ± 973.1	10,490.1	8,789.7 ± 1,829.8
Polar moment ⁷	17,091.1 ± 2,159.0	21,618.3	20,647.5 ± 7,515.4
Midshaft (n = 6)			(n = 7)
Total area	346.3 ± 26.6	489.3	360.4 ± 56.8
Cortical area	266.4 ± 23.7	264.6	237.0 ± 38.5
Medullary area	79.9 ± 17.0	224.7	123.3 ± 33.6
A-P 2nd moment	10,714.1 ± 1,026.3	15,550.5	9,436.1 ± 3,028.5
M-L 2nd moment	8,476.4 ± 1,714.2	15,078.4	9,972.0 ± 2,847.7
Polar moment	19,190.5 ± 2,617.7	30,628.9	19,408.1 ± 5,812.2
Mid-proximal (n = 7)			(n = 7)
Total area	345.1 ± 61.2	528.7	455.3 ± 79.3
Cortical area	243.1 ± 41.5	241.1	278.9 ± 72.3
Medullary area	102.0 ± 34.2	287.6	176.4 ± 29.0
A-P 2nd moment	8,589.7 ± 2,554.1	17,704.6	14,563.0 ± 5,995.1
M-L 2nd moment	9,479.9 ± 2,997.7	14,496.9	14,287.7 ± 6,236.8
Polar moment	18,069.6 ± 5,464.7	32,201.5	28,850.7 ± 12,101.9

¹ Composition of comparative samples is provided in Table 4. Cross-sectional geometric properties determined at 35% (mid-distal), 50% (midshaft), and 65% (mid-proximal) of humeral articular length measured from the distal end.

² Total area (TA; mm²): subperiosteal area of the cross-section (= cortical + medullary areas).

³ Cortical area (CA; mm²): area occupied by cortical bone tissue.

⁴ Medullary area (MA; mm²): area occupied by marrow cavity.

⁵ A-P 2nd moment (I_{AP}; mm⁴): second moment of area about a mediolateral axis passing through the center of the section.

⁶ M-L 2nd moment (I_{ML}; mm⁴): second moment of area about an anteroposterior axis passing through the center of the section.

⁷ Polar moment (J; mm⁴): polar moment of inertia of the section (=I_{AP} + I_{ML}).

pared to both Neandertal and early modern males. The narrowness of the fossa relative to epicondylar breadth results in relatively large medial and lateral pillars bounding the fossa (Table 5). Accordingly, the morphology of the distal epiphysis is more similar to that of modern humans than of Neandertals. The distal articular surface is also expanded in Vogelherd 3 (Table 3), but its size relative to humeral length or epicondylar breadth does not distinguish it from either group (Table 5).

Raw and standardized diaphyseal cross-sectional properties are provided in Tables 6 and 7, respectively. At the three diaphyseal levels studied, Vogelherd 3 has absolutely large total cross-sectional areas (Table 6), as well as generally elevated cortical tissue areas. The combination of thick cortical tissue and large cross-sectional total areas, indicating that the cortical tissue is distributed well away from the section centroid (geometric center) or from any neutral axis for bending that passes through that centroid, results in large values for the second moments of inertia (Table 6). When these geo-

metric properties are standardized to bone length, the true robusticity (relative bone strength) of Vogelherd 3 becomes more apparent (Table 7). Vogelherd 3 has standardized cortical areas (a measure of the resistance of the shaft to axial loads) intermediate between Neandertals and early modern males at the mid-distal and midshaft locations, not statistically significantly different from either comparative sample. At the mid-proximal level, Vogelherd 3 has a standardized CA value below, but again not significantly different from, the mean values of both comparative groups. At all diaphyseal levels, Vogelherd 3's measures of bending and torsional robusticity fall above the Upper Paleolithic male sample means, although the differences only reach statistical significance at midshaft. In the mid-distal shaft, Vogelherd 3 has robusticity measures that are generally comparable to those of the Neandertal sample, while at the two more proximal levels, Vogelherd 3 exceeds the Neandertal male means (although not significantly) in all measures of bending and torsional

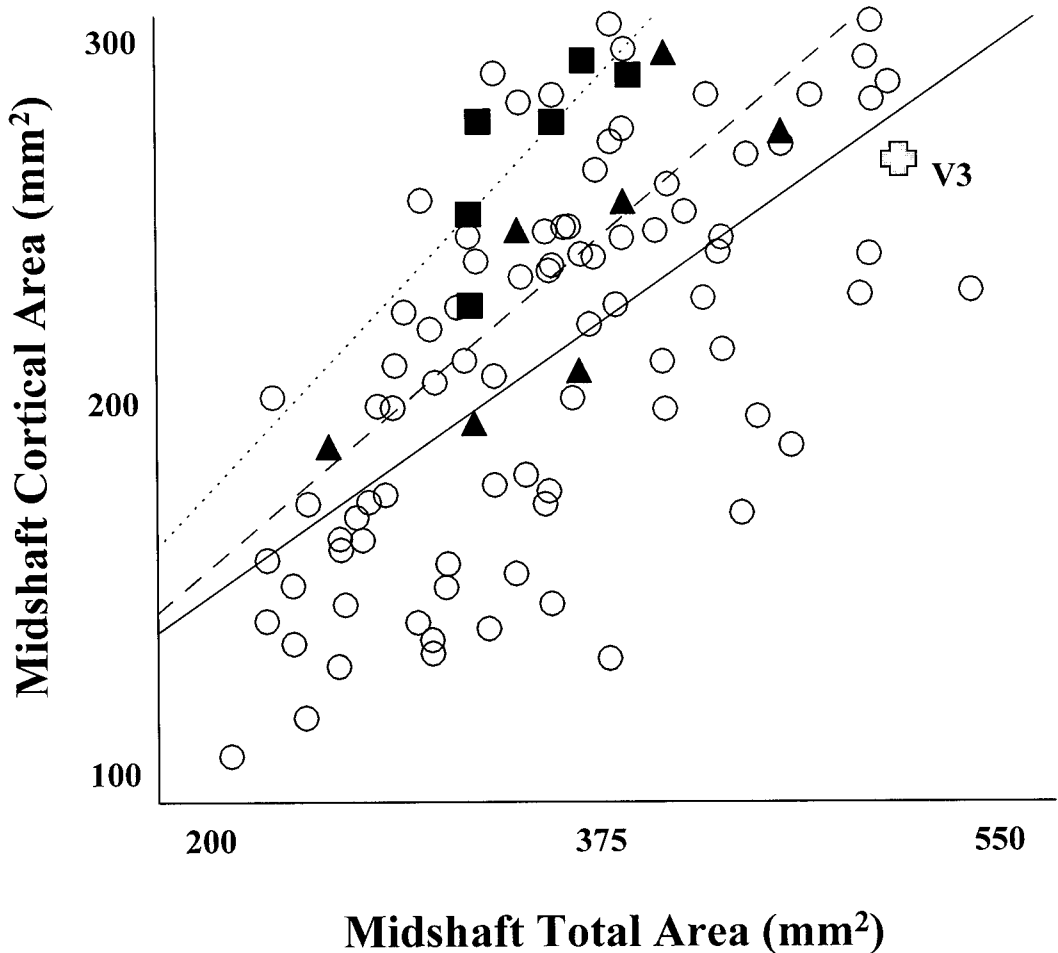


Fig. 10. Midshaft cortical area on total cross-sectional area in three groups of males: Neandertals (solid squares, dotted LS regression line $y = 25.98 + 0.694x$, $r = 0.777$); Early Upper Paleolithic (solid triangles, dashed LS regression line $y = 37.31 + 0.554x$, $r = 0.819$); and recent modern human (open circles, solid LS regression line $y = 52.00 + 0.457x$, $r = 0.638$). Recent human data are from Churchill (1994).

strength. The increased strength at midshaft (relative to early modern males) appears to be due to Vogelherd 3's having had relatively as much cortical bone as his contemporaries, but in the context of an expanded total cross-section (and hence an expanded medullary cavity). This serves to distribute more cortical bone tissue away from the axes of bending and the section centroid, making the humerus much stronger to bending and torsional loads at midshaft (indicated by I_{AP} , I_{ML} , and J), but about equal in terms of resistance to compressive and tensile loads (axial robusticity). Since most biomechanical loads on the

humerus involve bending and twisting and pure axial loads are rare, the enhanced second moments (bending and torsional robusticity) are the more salient measures of strength.

The canonical variates analysis was conducted with seven Neandertals and nine European early modern human male humeri, with the Vogelherd humerus being entered into the analysis as its own group (see Oxnard, 1972a,b; van Vark, 1976; Corrucini, 1978). All analyses were performed using JMP Version 3 (SAS Institute, 1995).

The first CVA was conducted on raw measurements and found two canonical axes

TABLE 7. Humeral robusticity (standardized cross-sectional properties): right humeri, males only¹

	Neandertals (n = 6) mean \pm SD	Vogelherd 3	Early Upper Paleolithic (n = 7) mean \pm SD
Mid-distal			
Axial robusticity ²	278.4 \pm 40.1	255.4	218.8 \pm 34.9
A-P bending robusticity ³	1,036.6 \pm 209.1	905.0	818.2 \pm 202.3
M-L bending robusticity ⁴	821.8 \pm 169.9	853.1	611.5 \pm 133.6
Torsional robusticity ⁵	1,858.4 \pm 362.0	1,758.1	1,430.2 \pm 324.2
Midshaft			
Axial robusticity	278.7 \pm 44.5	238.6	207.2 \pm 20.0
A-P bending robusticity	1,172.7 \pm 245.7	1,264.6	707.9 \pm 119.4*
M-L bending robusticity	932.4 \pm 263.1	1,226.2	755.2 \pm 140.0*
Torsional robusticity	2,105.1 \pm 496.2	2,490.9	1,463.2 \pm 246.4*
Mid-proximal			
Axial robusticity	266.1 \pm 50.9	217.4	230.6 \pm 48.4
A-P bending robusticity	1,032.3 \pm 219.6	1,439.8	978.3 \pm 274.2
M-L bending robusticity	1,155.0 \pm 335.3	1,179.0	979.3 \pm 336.2
Torsional robusticity	2,187.3 \pm 549.4	2,618.8	1,957.7 \pm 605.0

¹ Composition of comparative samples is provided in Table 4. Cross-sectional geometric properties determined at 35% (mid-distal), 50% (midshaft), and 65% (mid-proximal) of humeral articular length measured from the distal end.

² Axial robusticity: relative strength of the humerus to axial loads (compression, tension), calculated as $(CA/HAL^2) \times 10^5$.

³ A-P bending robusticity: relative strength of the humerus to bending in the anteroposterior plane (about a mediolateral axis passing through the center of the section), calculated as $(I_{AP}/HAL^4) \times 10^9$.

⁴ M-L bending robusticity: relative strength of the humerus to bending in the mediolateral plane (about an anteroposterior axis passing through the center of the section), calculated as $(I_{ML}/HAL^4) \times 10^9$.

⁵ Torsional robusticity: relative strength of the humerus to torsion and bending in general, calculated as $(J/HAL^4) \times 10^9$.

* Vogelherd 3 significantly different from sample mean at $0.05 \geq P > 0.001$. Test of single observation against sample means based on modified *t*-test (Sokal and Rohlf, 1981, p. 231).

TABLE 8. Results of the canonical variates analysis on raw humeral dimensions

Canonical axis	Eigenvalue	% between group variance explained	
1	20.578631	95.27	
2	1.021192	4.73	
Mean position of groups on	Canonical axis 1	Canonical axis 2	
Vogelherd 3	-1.74432	4.33331	
Neandertals	-5.01481 \pm 0.345467*	3.53563 \pm 0.272359*	
Early Modern humans	-2.97840 \pm 0.188386*	3.30419 \pm 0.263373*	
Eigenvectors	Canonical axis 1	Canonical axis 2	
Deltoid tuberosity width	0.1027648	-0.0354250	
Midshaft maximum diameter	-0.0251728	-0.1005195	
Midshaft minimum diameter	0.0211970	-0.0940307	
Midshaft cortical area	-0.1498478	0.4435848	
Midshaft medullary area	0.1580779	0.2475453	
Distodorsal medial pillar diameter	0.2275560	-0.1000986	
Distodorsal lateral pillar diameter	0.0637826	-0.0131795	
Epicondylar breadth	-0.1116123	-0.0637704	
Distal articular breadth	-0.0204559	0.0897624	

* Vogelherd 3 significantly different from sample mean at $0.05 \geq P > 0.001$. Test of single observation against sample means based on modified *t*-test (Sokal and Rohlf, 1981, p. 231).

that account for the between group variance (Table 8), with the first axis accounting for slightly more than 95% of the observed variance. The major contrast in the first vector is between distodorsal medial pillar diameter, midshaft medullary area, and deltoid tuberosity width (all with positive values) and midshaft cortical area and epicondylar breadth (with negative values). This contrast effectively separates Neandertal and early modern humeri, with Neandertal hu-

meri being characterized by relatively small medullary areas, narrow deltoid tuberosities, narrow pillars bounding the olecranon fossa, and large cortical areas and distal epiphyses. Vogelherd 3 occupies a position on canonical axis 1 distant from the Neandertal and early modern human samples (Table 8), and its score on this axis is significantly different than the means of both samples. Nevertheless, the Vogelherd humerus is not positioned between the com-

TABLE 9. Results of the canonical variates analysis on log-shape humeral dimensions

Canonical axis	Eigenvalue	% between group variance explained		
1	13.7668702	>88.78		
2	1.7376256	11.21		
3	0.0000526	<0.01		
Mean position of groups on	Canonical axis 1	Canonical axis 2		
Vogelherd 3	7.14708	7.18969		
Neandertals	9.78935 \pm 0.368807*	8.24069 \pm 0.291595*		
Early Modern humans	8.11440 \pm 0.151612*	8.53599 \pm 0.247434*		
	Eigenvectors for axis 1	Loadings for axis 1	Eigenvectors for axis 2	Loadings for axis 2
Deltoid tuberosity width	44,012.1996	-0.8674	361,134.431	0.0923
Midshaft maximum diameter	44,019.3600	0.8286	361,132.637	-0.0946
Midshaft minimum diameter	44,013.6631	0.4121	361,140.174	0.2579
Midshaft cortical area	44,015.7087	0.9011	361,119.063	-0.0771
Midshaft medullary area	44,011.9108	-0.5371	361,125.583	-0.3596
Distodorsal medial pillar diameter	44,011.0025	-0.4155	361,135.542	0.2754
Distodorsal lateral pillar diameter	44,010.9352	0.2362	361,130.578	-0.1589
Epicondylar breadth	44,028.9497	0.9382	361,151.157	0.0255
Distal articular breadth	44,011.8885	0.7834	361,123.090	0.0301

* Vogelherd 3 significantly different from sample mean at $0.05 \geq P > 0.001$. Test of single observation against sample means based on modified *t*-test (Sokal and Rohlf, 1981, p. 231).

parative samples on axis 1, but in fact falls beyond the early modern mean in the direction away from the Neandertals. Since Vogelherd 3 is close to the Neandertal male mean in epicondylar breadth (Table 3) and midshaft cortical area (Table 6), its distance from the Neandertals on canonical axis 1 must be largely driven by its wide distodorsal medial pillar and deltoid tuberosity and its large medullary area.

The second canonical axis, which accounts for roughly 5% of the between-group variance, contrasts midshaft cortical and medullary areas (with positive values) with distodorsal medial pillar diameter and the maximum and minimum diameters at midshaft (all with negative values) (Table 8). Canonical axis 2 does not effectively separate Neandertal and early modern males (their mean scores are not significantly different), but instead highlights differences between Vogelherd 3 and both comparative groups.

To see if the results differed once size variance was removed, we also ran the CVA on log-shape variables (Darroch and Mosimann, 1985). Again, two axes accounted for most of the between-group variance (Table 9), although a third axis, accounting for less than 0.01% of the variance, was also identified (only the Eigenvectors for the first two axes are reported in Table 9). Inspection of

the loadings (or structure coefficients, the correlation between each variate and the canonical axis) on the first axis reveals a contrast similar to that seen on the first axis of the CVA on the raw data. Namely, distodorsal medial pillar diameter, midshaft medullary area, and deltoid tuberosity width (all with negative loadings) are contrasted with midshaft cortical area, epicondylar breadth, midshaft maximum diameter, and distal articular breadth (all with positive loadings). Again, the first axis serves to distinguish Neandertal from early modern humeri, and again Vogelherd 3's score on this axis is significantly lower than the mean score of either comparative group, yet is closer to the early modern sample than it is to Neandertals. As with the CVA on raw variates, the analysis of log shape variates produced a second axis that does not differentiate Neandertals and early modern humans, but that does serve to distinguish Vogelherd 3 from both groups.

DISCUSSION

The most striking feature of the Vogelherd 3 humerus is its large, rugose, and projecting deltoid tuberosity. The overall stoutness and rugose muscle scarring of this specimen were what led to initial claims that it may represent a Neandertal, and undoubtedly the enlarged, rugged deltoid tuberosity must have

contributed to this impression. Ironically, it is the morphology of the deltoid tuberosity that most clearly distinguishes the Vogelherd 3 humerus from those of Neandertals. In its absolute and relative width, and in its crest configurations, the deltoid tuberosity of Vogelherd 3 is most similar to those of early modern humans from later Aurignacian and Gravettian contexts.

One issue that must be addressed is the taxonomic valence of deltoid tuberosity morphology. Given that muscle scar size and rugosity plastically respond to repetitive muscle use (Hoyte and Enlow, 1966; Yamada et al., 1988; Hawkey, 1988), it is reasonable to question the use of this trait as a taxonomic marker. It has also been argued that deltoid tuberosity width is determined by humeral torsion angle (which cannot be directly measured on the Vogelherd humerus), such that the lower the angle, the narrower the deltoid tuberosity (Carretero et al., 1997). Given that variation in humeral torsion angle may reflect interspecific variation in activity levels and/or chest shape (see Churchill, 1994), this further calls into question the utility of deltoid tuberosity morphology in classifying isolated humeri.

Churchill (1994) examined the effects of body form (size, chest shape, and measures of muscularity, articular robusticity, and diaphyseal robusticity) on variation in deltoid tuberosity width through partial correlation analysis conducted on a large pooled sample of fossil and recent humans. No significant partial correlations were found between deltoid tuberosity width and any other measure of body form (with all other body form measures held constant). The only upper limb variable Churchill found to be significantly related to deltoid width was the relative position of the deltoid tuberosity (taken as the distance from the proximal-most point on the head to the distal-most point of the deltoid tuberosity, divided by humeral articular length), which is understandable given that the farther distally the insertion for *M. deltoideus* extends down the shaft, the wider the muscle scar is likely to be at 5/12 humeral length. Neandertals tend to have slightly more distally positioned deltoid tuberosities (Churchill, 1994); thus, one

would expect their tuberosities to be *wider*, not narrower, than in modern humans. As for humeral torsion angle, there does exist a significant difference in mean angle between Neandertals and early modern Europeans (mean of seven Neandertal males and females = $133.4 \pm 16.7^\circ$; mean of 14 early Upper Paleolithic males and females = $144.4 \pm 9.1^\circ$). However, we were unable to detect a significant correlation between humeral torsion angle and either raw deltoid tuberosity width ($r = 0.0125$) or deltoid index ($r = -0.090$) in a mixed-sex sample of 304 recent and fossil humans (including Neandertals: data from Churchill, 1994). Thus there appears to be no direct relationship between the width of the deltoid tuberosity and potentially confounding features of body form or activity, and we feel confident that this feature has utility in identifying Vogelherd 3 as a modern human humerus.

The other features that differentiate Vogelherd 3 from the Neandertal sample, such as the reduced percent cortical area in the midshaft and mid-proximal humeral cross-sections and the morphology of the medial and lateral dorsal pillars of the distal epiphysis, support the impression that this specimen derives from an anatomically modern human. The few features in which Vogelherd 3 is similar to Neandertals are features that are plastic to environmental influences, and thus potentially untrustworthy for the task of classification. As noted above, the size and rugosity of muscle attachment sites are responsive to repetitive use (Hoyte and Enlow, 1966; Yamada et al., 1988; Hawkey, 1988). Thus, while it is true that Vogelherd 3 exhibits an *M. pectoralis major* insertion scar that is well above the mean breadth for early Upper Paleolithic males, it is also the case that similarly wide entheses can be found among modern humans. For example, although a mixed-sex sample of 21 German Neolithic humeri (Smith, unpublished data) produced a mean pectoralis major index ($100 * M. pectoralis major \text{ breadth/midshaft maximum diameter}$)³ below that of Vogelherd 3 and the

³ The same results were obtained when *M. pectoralis major* breadth was examined relative to humeral length.

Neandertal male sample (34.7 ± 7.0 vs. 51.0 (Vogelherd 3) and 38.5 ± 5.9 (7 male Neandertals)), 24% of the specimens had index values equal to or above the Neandertal mean (Neolithic range, 19–48.5). The size of the *M. pectoralis major* insertion scar is obviously highly variable within populations and of little taxonomic value.

Likewise, the mechanical strength of long bones has been shown to change with changes in habitual limb use and loading patterns (see Trinkaus et al., 1994). Accordingly, postcranial robusticity has been found to be an unreliable taxonomic marker in differentiating archaic from early modern human long bones (Pearson and Grine, 1996; Churchill et al., 1996). While it is the case that long bone diaphyseal robusticity shows a trend for reduction in humans across the Quaternary (Ruff et al., 1993), and that early modern Europeans are on average less robust than Neandertals (Table 7), a high degree of within-group variation in robusticity (reflecting as it does idiosyncratic loading histories) makes the trait taxonomically unreliable. It is important to note as well that while measures of Vogelherd 3's humeral bending and torsional rigidity are comparable to or above the mean values observed in Neandertal males (Table 7), Vogelherd 3 attained this strength by having had a moderate amount of cortical tissue distributed far away from the center of the diaphyseal cross section (the pattern characteristic of fossil and recent modern humans: Churchill, 1994). Neandertals, on the other hand, tend to have achieved similar levels of bone strength by having had large amounts of cortical tissue in the context of a smaller overall cross section (with a smaller medullary cavity: Churchill, 1994). Thus while Vogelherd 3's humeral robusticity may be similar to that of Neandertal males, the underlying morphology is more closely aligned with modern humans.

The Vogelherd humerus evidently derived from a robust, muscular individual, yet there is nothing that clearly indicates the retention of Neandertal features. In this respect, the Vogelherd humerus is similar to the postcranial material recovered from Aurignacian contexts at Mladeč Cave (Czech Republic) (Smith et al., 1989). Like Vogelherd 3, some aspects of the Mladeč postcranial material

evince skeletal hypertrophy (most notably, the size of the joint surfaces: Wolpoff, 1992), but the overall morphology is more modern than archaic. This includes nonstenotic long bone diaphyses with reduced cortical thickness, and the clear absence of typical Neandertal features (such as narrow humeral deltoid tuberosities, medially oriented radial tuberosities, and absence of femoral pilasters) (Smith et al., 1989). At both Mladeč and Vogelherd, possible Neandertal-reminiscent features are more readily identifiable in the cranial than postcranial material (see Smith et al., 1989; Frayer, 1992; Wolpoff, 1992; Frayer et al., 1993).

The Vogelherd 3 humerus adds to the list of anatomically modern human fossils from early Aurignacian contexts. For the earliest (Würm interstadial) Aurignacian, this list includes an adult calotte from an undated but presumably interstadial level at Cioclovina (Romania: Rainer and Simionescu, 1942), the large sample from Mladeč (Czech Republic: Szombathy, 1925), and the cranial and postcranial fragments from Zlatý Kůň and Svatý Prokop (Czech Republic: Svoboda et al., 1996). The Vogelherd 3 humerus reinforces the pattern of association between unequivocally Aurignacian cultural assemblages and people with fundamentally modern morphology which is widely argued to characterize Europe between 40 and 30 kyBP.

The significance of the association of Neandertal fossils with Aurignacian artifacts at Vindija Cave remains uncertain. Claims of cryoturbational or bioturbational mixing of lower Mousterian and higher Aurignacian horizons in Vindija level G₁ (d'Errico et al., 1998) can be reasonably ruled out on taphonomic and stratigraphic grounds (Karavanić and Smith, 1998). While there are only 16 typologically diagnostic lithics from this level (which include both characteristic Mousterian (e.g., denticulates and side scrapers) and Aurignacian (including an endscraper on an Aurignacian blade) forms, it has produced characteristic Aurignacian bone tools (including massive-base and split-base points). However, the utility of these artifacts as *fossiles directeurs* for the Aurignacian of East-Central Europe has not been established (Karavanić and Smith, 1998), and at present it is uncertain

whether the Vindija G₁ assemblage represents an early Aurignacian comparable to that found elsewhere in Europe, a Central European regional variant of the Aurignacian ("Olschewian;" see Karvanić and Smith, 1998), a Szeletian component (Miracle, 1998), or a late Mousterian that incorporates Aurignacian tools obtained through contact with (possibly) contemporaneous Upper Paleolithic peoples living at nearby sites like Velika Pécina. At present, the evidence from Vindija G₁ does not represent a compelling exception to the pattern of association between the Aurignacian and modern morphology in Pleistocene Europe.

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